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Abstract: Tracks of small quadrupedal ornithischians with five manual and four pedal digits have been recorded from sedimentary rocks near the Late Jurassic–Early Cretaceous (Tithonian–Berriasian) boundary in NE Thailand and British Columbia. These are compared with larger tracks of gracile, quadrupedal ornithopods from the earliest Cretaceous of Spain and smaller tracks of a quadruped of unknown age from Zimbabwe. The Thai and Canadian tracks are similar to the Early Jurassic (Liassic) ichnogenus *Anomoepus* and the small ornithopod tracks from the Late Jurassic of Spain. They are the only known post-Liassic ornithischian tracks in which up to five discrete manus digit impressions are clearly visible. Based on strong heteropody (manus much smaller than pes) in all cases we infer an ornithopod trackmaker rather than another ornithischian. The scattered, but widespread earliest Cretaceous occurrence of this ichnotaxon, herein assigned to *Neoanomoepus perigrinatus* ichnogen. and ichnosp. nov., on the basis of type material from Canada, suggests that these hitherto unknown earliest Cretaceous ichnofaunas may represent a radiation of small basal ornithopods (pes length less than 15 cm), appearing before the widespread radiation of large ornithopods (pes length up to 60 cm or more) later in the Neocomian (Valanginian–Barremian), Aptian–Albian and Late Cretaceous. The primitive condition of the trackmaker is indicated by the pedal and manual morphology, which consists of four and five digits respectively that are not enclosed by well-developed fleshy padding or integument. In contrast, all larger Cretaceous ornithopod tracks, mostly from post-Berriasian strata, have only three pedal digits enclosed in fleshy pads and a manus in which all functional digits are reduced and enclosed by substantial flesh.

Trackways of small ornithopod dinosaurs are still comparatively rare. The most famous, and first-described, example of a trackway with what appears to be unequivocal ornithopod or basal ornithischian characteristics (five-toed manus and four-toed pes) is the well-known Early Jurassic ichnogenus *Anomoepus* (Hitchcock 1848; Lull 1953; Olsen & Rainforth 2003). This ichnogenus (Fig. 1) is well known from the early Jurassic of the eastern USA and may be abundant in southern Africa (Ellenberger 1972) but was, until recently, relatively poorly known from other regions such as the western USA (Lockley & Hunt 1995; Lockley & Gierlinski 2006), Europe (Avanzini *et al.* 2001; Gierlinski 1991; Gierlinski *et al*. 2004; Lockley & Meyer 2000) and Australia (Thulborn 1994). *Anomoepus* is characterized, in well-preserved examples, by a four-toed pes, sometimes with metatarsal impressions, and a five-toed manus. In many cases, however, *Anomoepus* is hard to identify with confidence unless both manus and pes tracks are found (Lockley & Gierlinski 2006). In many cases the trackmaker was progressing bipedally, and hallux (digit I of the pes) is inconspicuous and may not be impressed. Moreover, if not well preserved it may be difficult to distinguish *Anomoepus* tracks from a number of other tridactyl or tetradactyl dinosaur footprints. However, there may be some clues to the ornithischian affinity of incomplete *Anomoepus* or *Anomoepus*-like ichnites in the general configuration of the trackway. As indicated by Lockley (1999), ornithopods typically, indeed consistently, have trackways that are relatively wide in comparison with those of theropods and consistently take shorter steps, with shorter (wider) pes tracks that toe inward.

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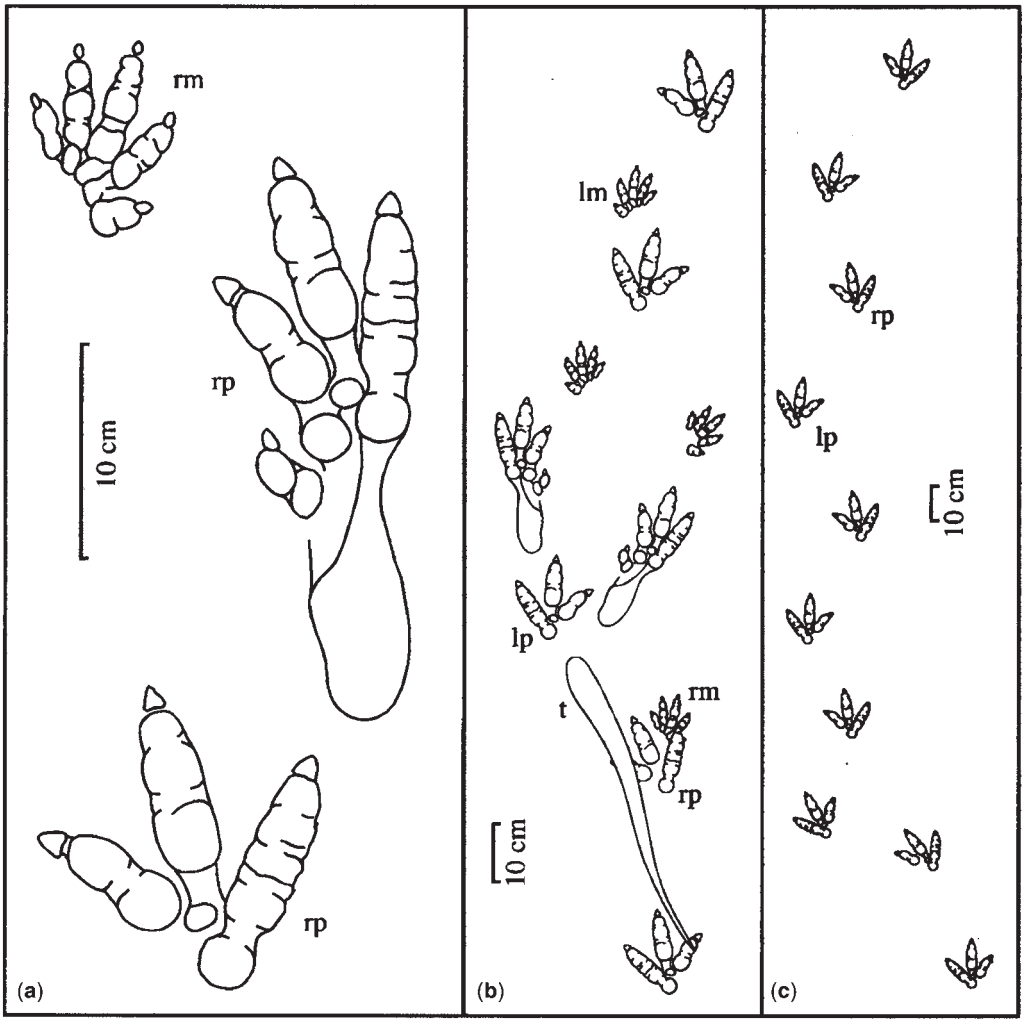

Fig. 1. Type *Anomoepus* from the Early Jurassic of New England (after Olsen & Rainforth 2003, fig 19.5). (**a**) An idealized composite of walking pes and sitting manus and pes with metatarsal impressions; (**b**, **c**) composite trackways showing quadrupedal and bipedal impressions, respectively. rm, right manus; rp, right pes; lm, left manus; lp, left pes; t, tail.

Despite this distinctive combination of characters there are few known examples of post-Early Jurassic tracks that have been assigned unequivocally to *Anomoepus*. Moreover, with the possible exception of the enigmatic, presumed heterodontosaurid track *Delatorrichnus* from the Middle Jurassic of Argentina (Casamiquela 1964), there is only one reported example of a Late Jurassic ornithopod track that reveals quadrupedal progression. This is a hitherto undescribed specimen from the Late Jurassic of Asturias (García Ramos *et al*. 2006; Lockley *et al*. 2009). *Dinehichnus* is the only other formally named Late Jurassic track attributed to an ornithopod (Lockley *et al.* 1998). It is not until the Cretaceous that we find abundant ichnological evidence of quadrupedal and bipedal ornithopods in many regions including Asia (You & Azuma 1995; Lockley & Matsukawa 1998). However, most of the larger quadrupedal forms had a hoof-like manus without clear separation of the digit traces. Other than the Cretaceous material described herein, the only other footprints of small quadrupedal ornithopods, with distinct digit impressions, hitherto named from the Early Cretaceous are *Hypsiloichnus* (Stanford *et al.* 2004). All other tracks of quadrupedal Cretaceous ornithopods

indicate much larger trackmakers whose hand and foot morphology bears little or no resemblance to that of the *Anomoepus* trackmaker.

Trackways of large ornithopod dinosaurs are fairly well known in the Cretaceous. Most, however, are large with three well-padded pes impressions indicating the derived condition typical of iguanodontids or hadrosaurs (e.g. *Iguanodontipus*, Sarjeant *et al.* 1998). Some indicate quadrupedal progression, but in such cases the manus is revealed to be a relatively small sub-circular to oval hoof-like impression that rarely reveals any differentiation of digit traces.

Only recently have reports emerged of Cretaceous trackways that evidently represent small quadrupedal ornithopods that exhibit the primitive, *Anomoepus*-like, condition of four pedal and five manual digits (Fig. 2). These discoveries have been made in such widely divergent localities as Thailand (Buffetaut & Suteethorn 1993; Le Loeuff *et al.* 2002; Matsukawa *et al.* 2006), Zimbabwe (Lingham-Soliar & Broderick 2000) and Canada (this study). Other distinctive ornithopod morphotypes have been recorded from Spain (Perez-Lorente *et al.* 1997). The primary purpose of this paper therefore is to describe these Cretaceous examples in detail and discuss their ichnotaxonomic status. A secondary objective is, where possible, to place the tracks in their biostratigraphic, palaeobiogeographical and palaeoecological context and discuss the extent to which they may shed light on the timing of the Early Cretaceous ornithopod radiation.

Track material and geological context

Thailand specimens

Tracks that closely resemble the Canadian specimens are known from the Phra Wihan Formation of NE Thailand at a site known as Hin Lat Pa Chad (Buffetaut & Suteethorn 1993; Le Loeuff *et al.* 2002; Matsukawa *et al.* 2006). The tracks occur at a single isolated locality in a jungle region. The outcrop consists of a single bedding

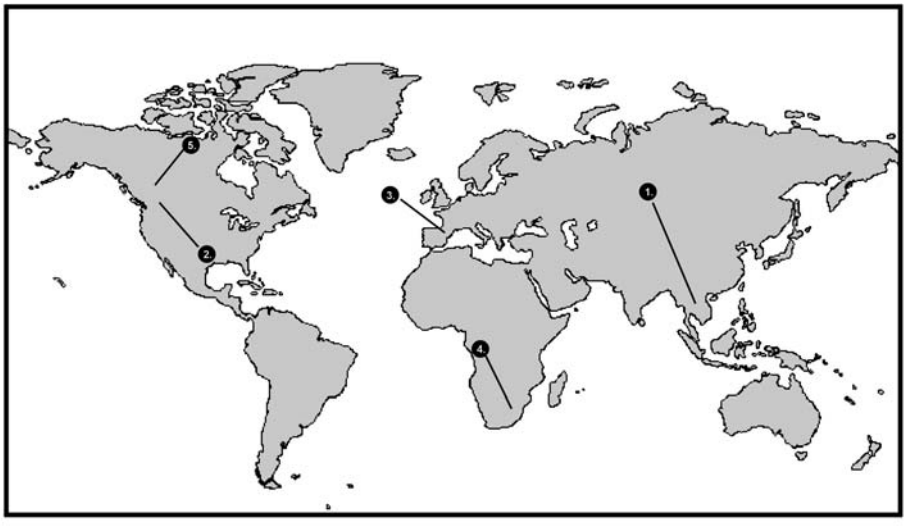

Fig. 2. Locality map showing the type locality for *Neoanomoepus periginatus* ichnogen. et ichnosp. nov. in British Columbia, and the occurrence of other probable *Neoanomoepus* or *Neoanomoepus*-like ichnites from Thailand, Zimbabwe, Spain and Canada.

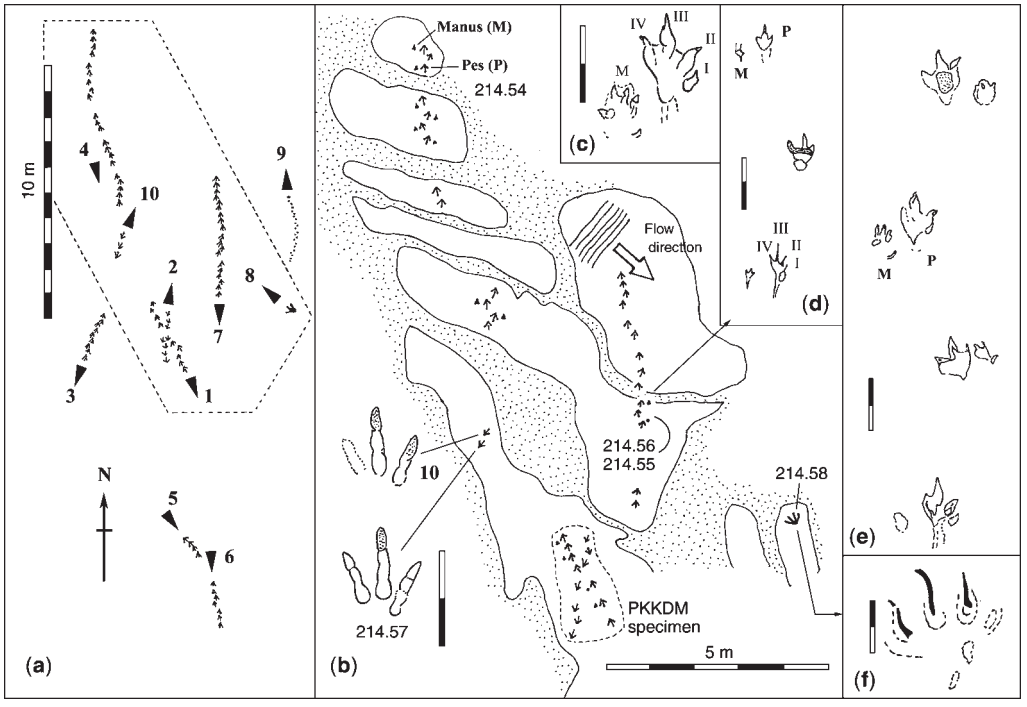

Fig. 3. Tracks from the Hin Lat Pra Chad site in Thailand (after Matsukawa *et al.* 2006). (**a**) Preliminary map produced in local field guide with numbered trackway segments 1–10. Trackway 1 may be a continuation of 4, and 6 may be a continuation of 7. (**b**) Detailed map of northern section showing trackways 1, 2, 4, 7, 8 and 10 (with detail of 10), current ripple vector, and source of track replicas (University of Colorado at Denver 214.54–58) and Phu Kum Kao Dinosaur Museum (PKKDM) replica. (**c**) Composite of ornithischian manus (M)–pes (P) set from trackway 1, showing 4 pes and 5 manus digit impressions. (**d**) Detail of trackway 7 also showing 4 pes digit impressions. (**e**) Detail of trackway 4. (**f**) Detail of large track (trackway 8). All track detail scale bars 10 cm.

plane of about 25 m × 10 m with 10 trackways mostly trending from north to south (Fig. 3). As noted by Buffetaut & Suteethorn (1993, p. 77), some trackways 'sometimes show a small, apparently tridactyl manus impression lateral to the pes impression … [which] … together with the general shape of the footprints suggest that they may have been left by ornithischians'. We agree with this interpretation generally, but note that the pes tracks sometimes show faint impressions of the hallux and are therefore tetradactyl, and that at least one manus track is also tetradactyl, and may be interpreted as pentadactyl.

Le Loeuff *et al.* (2002, p. 291) considered the manus tracks 'reminiscent' of *Anomoepus intermedius* and *A. scambus*, but they stopped short of applying these names to the illustrated material (Le Loeuff *et al.* 2002, fig. 4). According to Olsen & Rainforth (2003), *A. intermedius* is a synonym of *A. scambus*, which is the only recognizable ichnospecies in the ichnogenus *Anomoepus*. However, Lockley & Gierlinski (2006) disputed the claim that the ichnogenus is monospecific.

The Thai material was re-examined by Matsukawa *et al.* (2006), who illustrated two trackways (Fig. 3) with both manus and pes footprints demonstrating that in some cases the former are pentadactyl and the latter tetradactyl. In that paper, Matsukawa *et al.* (2006) reproduced a previously unpublished map of the site in which 10 trackways were numbered. Comparison of these two maps (Fig. 3a and b), which use the same numbering scheme, reveals that trackways 3, 5, 6 and 9 are not included because they were covered by sediment at the time they were studied by Matsukawa *et al.* (2006). Moreover trackways 3, 5 and 6 are probably continuations of other trackways such as 1, 4 or 7. Nevertheless, these trackways (1, 4 and 7) all have associated manus impressions (Fig. 3c–e), whereas other trackways (e.g. 2 and 3) indicate biped progression on a functionally tridactyl pes, probably attributable to ornithopods. The possibility that some tridactyl tracks are theropodan cannot be discounted. One large tetradactyl track, with curved digit impressions, may be attributable to a crocodilian (Fig. 3f).

The Phra Wihan Formation is considered as Neocomian in age, or may be Berriasian. The probable age for the Phra Wihan Formation given by Buffetaut & Suteethorn (1993) is Late Jurassic. However, in a later paper (Buffetaut *et al.* 1997), they gave a revised age of early Cretaceous (Berriasian–Barremian) based on palynomorphs (Racey *et al.* 1994, 1996). This age estimate, followed by Le Loeuff *et al.* (2002) and Matsukawa *et al.* (2006), is further supported by Racey & Goodall (2009).

Canadian specimens

Well-preserved and diagnostic small ornithischian ichnites are herein reported from the coal-bearing Mist Mountain Formation of the Elk Valley Coal region in SE British Columbia, Canada. About two dozen clear tracks are preserved as natural casts on the underside of a sandstone slab of about 3 m^2 (Figs 4–6). In total almost 100 tracks may be discerned by careful observation of the specimen, mould and replica under controlled lighting conditions. Several trackway segments are discernible, including at least three with three or more consecutive manus–pes sets (Fig. 5, Table 1). The precise stratigraphic location from which the tracks originate is not known. However, the approximate location, within the Fording River Coal mine, is known, and all the strata in the mine are Tithonian to Berriasian. The tracks are thought to originate from the Berriasian part of the section. The predominant lithology in this region is a coal-bearing sequence consisting of grey mudstones and siltstones with intercalated buff-coloured sandstone and coals (Bustin & Smith 1993). Tracks are abundant and include a variety of tridactyl tracks attributable to bipedal theropods, bipedal ornithopods and possibly water- or shore-birds (McCrea & Buckley 2005*a*). A few isolated sauropod tracks and one trackway have also been recorded (McCrea *et al.* 2005). As many as 80 track-bearing specimens have been set aside as outdoor displays near the mine entrance and more than a dozen specimens have been replicated for scientific study (see reference to specimens below). Plant fossils are also abundant, and locally moulds of freshwater unionid or unionid-like clams can be found.

The discovery of this important slab appears to confirm the report of Currie (1989, p. 294), who suggested that a trackway of a tridactyl biped, with inward pes rotation, from the Mist Mountain Formation, British Columbia, could be 'identified as *Anomoepus*'. However, this trackway, in the Tyrrell Museum (TMP 85.105.1), reveals no diagnostic manus tracks. Nevertheless, Currie's identification was prescient given the quadrupedal trackway with manus traces described herein.

Institutional abbreviations for replicas used in the systematic descriptions (below) are FGM for Fraser–Fort George Regional Museum, British Columbia; and CU for the University of Colorado at Denver, Dinosaur Tracks Museum.

Trackways from Spain

Although there are a number of reports of trackways of quadrupedal ornithopods from the Early Cretaceous of Spain, and other parts of Europe, North America and Asia, almost all examples other than those cited above refer to large tracks with well-rounded manus impressions in which

Fig. 4. Photograph of large *Neoanomoepus* track-bearing slab (field number A48) from Mist Mountain Formation, British Columbia. It should be noted that the tracks are preserved as natural casts. (Compare with Fig. 5.)

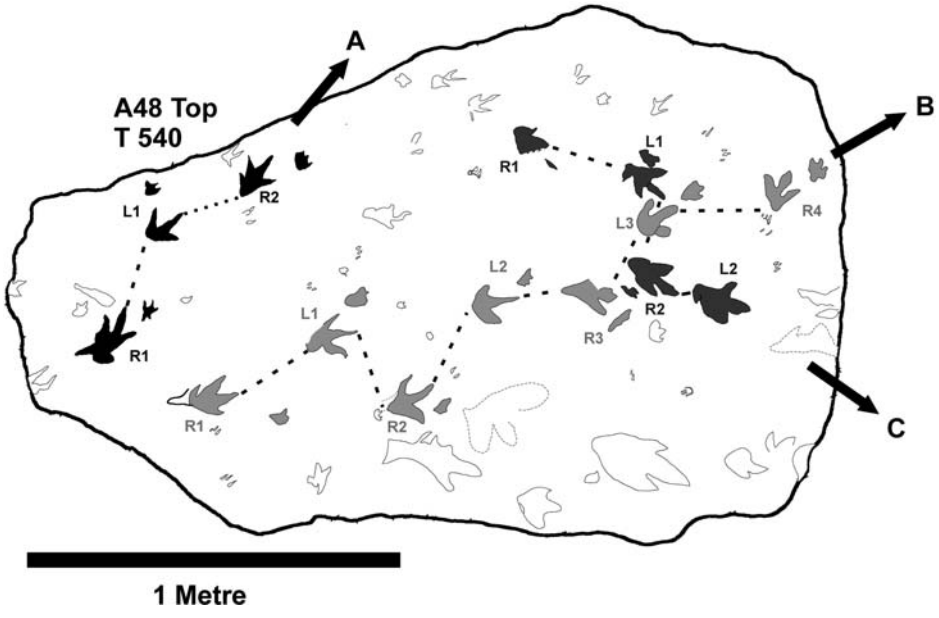

Fig. 5. Map of large track-bearing slab (field number A48) from Mist Mountain Formation, British Columbia. (Compare with Fig. 4, but note reversal to show non-natural cast aspect.) Trackway A is holotype for *Neoanomoepus* (see Figs 6 and 8). Details of trackways A–C are shown in Figure 8. Replica of complete slab in Fraser–Fort George Regional Museum (FGM 002.01.20).

Fig. 6. Photograph of the manus–pes set R1 from trackway A, the holotype of *Neoanomoepus* (FGM 002.01.20 and CU 199.22) (compare with trackway A of Fig. 5).

Table 1. *Measurements for standard trackway parameters for three* Neoanomoepus *trackways from the Mist Mountain Formation*

Track number	Pes L:W	Manus L:W	Step	Stride	Pace Ang.
A R 1	(19.0):9.8	4.2:6.4	–	–	–
A L 2	12.0:10.5	4.0:4.4	29.4	55.0	142
A R 2	10.0:13.7	4.1:4.8	27.3	–	–
B R 1	19.2:10.7	3.5:5.0	–	–	–
B L 1	(14.2):11.7	(4.5):(7.0)	36.1	52.5	107
B R 2	(14.5):13.5	3.0:5.5	25	44.0	90
B L 2	13.0:11.0	3.0:5.5	32.5	54.3	132
B R 3 ?	14.8:11.4	2.5:(3.5)	26.3	48.7	135
B L 3 ?	12.0:11.0	4.7:6.8	28.5	57.2	143
B R 4 ?	11.5:10.5	5.1:6.6	31.6	–	–
C R 1	(16.0): –	–	–	–	–
C L 1	13.9:10.5	3.8:6.1	32.3	47.0	109
C R 2	16.0:9.8	2.5:5.4	25.5	37.0	115
C L 2	16.1:11.4	–	19.5	–	–
Mean	–	–	31.1	49.5	122

L, length; W, width; Pace Ang., pace angulation for pes. Step measurements given for pes in row corresponding to completed step. Stride for pes given in row between two left or right footprints forming stride. Tracks with prefix A are from holotype trackway: those with B and C prefixes are paratypes (L, left; R, right). Brackets refer to measurements of tracks that are poorly, or incompletely, preserved.

individual manual digit traces are not differentiated or discernible. One exception of possible interest is the Tithonian–Berriasian ornithopod trackway reported by Perez-Lorente *et al.* (1997) from Las Cerradicas, Spain (see Lockley & Meyer 2000, fig. 8.4; Lockley & Wright 2001). This example is selected because it was, previously, the smallest and earliest described trackway of a quadrupedal ornithopod from the Cretaceous. One of us (M.G.L.) had the opportunity to observe these tracks and obtain accurate scale tracings (Fig. 7), which compare favourably with the largest trackways of *Dinehichnus* from the Late Cretaceous of NE Arizona. (Fig. 7). We present only a brief comparative analysis below, as the site is currently under investigation by others (see Acknowledgements). We conclude that in several respects the Cerradicas tracks are intermediate in character between *Dinehichnus* tracks and larger ornithopod tracks such as *Iguanodontipus* (Sarjeant *et al.* 1998). The ichnotaxonomic interpretation of these tracks is problematic for several reasons. The pes tracks are elongate and segmented with sharp claw traces, which make them morphologically convergent with theropod tracks, and similar to the recently described ichnogenus *Asianopodus* (Matsukawa *et al.* 2005). Furthermore, the Cerradicas pes tracks, which average about 22–23 cm in length, are considerably larger than the examples described from Canada and Thailand; however, they retain some of the primitive characteristics of *Anomoepus*, such as discrete phalangeal pads and relatively sharp claw traces. However, there is no trace of a hallux on the pes. Likewise, the manus is not robust and rounded or oval as in most large iguanodontid and hadrosaurid tracks, but is instead gracile and elongate with a rhomboidal shape, lacking clearly differentiated digit impressions, although blunt digit tip traces are inferred.

Trackways from Zimbabwe

Lingham-Soliar & Broderick (2000) reported an enigmatic dinosaurian trackway from the Mesozoic Dande Sandstone Formation, which is broadly dated as ?Early Jurassic to Mid-Cretaceous. This ichnite might be considered similar to *Delatorrichnus* (G. Gierlinski, pers. comm.). The trackway consists of 10 small pes tracks (about 5 cm long) and corresponding small manus tracks (2–3 cm long) associated with eight of the 10 pes tracks (Fig. 8). In this regard the tracks are similar in size to the smallest of the Thailand trackways. A second trackway consists of five or six small pes tracks, also about 5 cm long, with no associated manus.

Lingham-Soliar & Broderick (2000) suggested that the tracks might be similar to the Late Triassic ichnogenus *Atreipus* because of the tridactyl manus and pes. As stated above, there are very few trackways attributable to small quadrupedal dinosaurs, or dinosaur relatives. Indeed, prior to the discovery of the previously unnamed Thailand specimens (Le Loeuff *et al.* 2002; Matsukawa *et al.* 2006) and the Canadian tracks herein assigned to *Neoanomoepus*, the only small quadrupedal tracks that

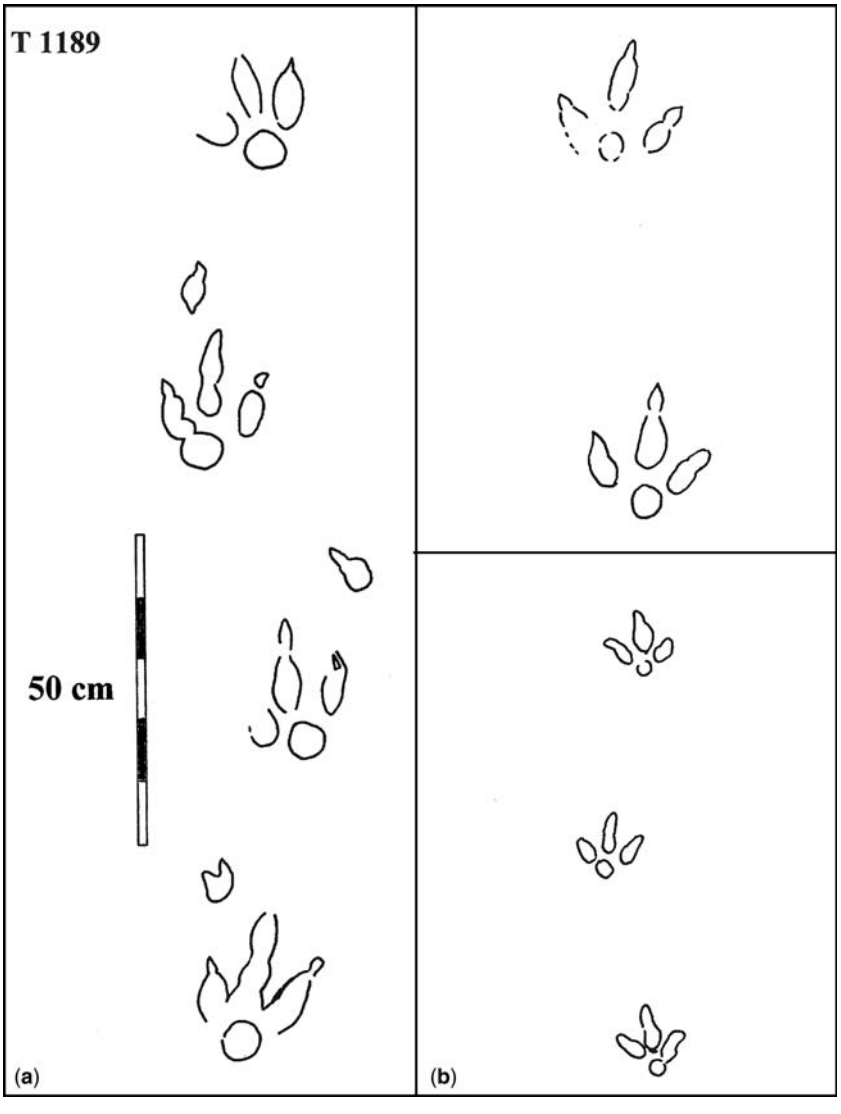

Fig. 7. (**a**) Trackway of quadrupedal ornithopod trackway from Cerradicas, Spain, based on CU Denver tracing T 1189, compared with (**b**) large and small bipedal *Dinehichnus* trackways, from the Late Jurassic of NE Arizona (Lockley et al. 1998).

had been confidently attributed to ornithischian trackmakers were *Anomoepus*, *Delatorrichnus* and *Hypsiloichnus*. The Late Triassic ichnogenus *Atreipus* (Olsen & Baird 1986) is also considered dinosaurian (ornithischian) by some researchers, but may also be attributed to a non-dinosaurian archosaur (Thulborn 1990, and citations therein). For these reasons a Late Triassic or Early Jurassic age for the Zimbabwe material was considered probable. However, the age of the Dande Sandstone Formation is poorly known, and could be Cretaceous in part. Possible trackmakers such as the heterodontosaurids survived until the earliest Cretaceous.

Systematic ichnology

General observations

Anomoepus (Hitchcock 1848), from the Lower Jurassic of the Connecticut Valley region, is one of the best-preserved examples of a distinctive dinosaur track. It forms the basis of the family

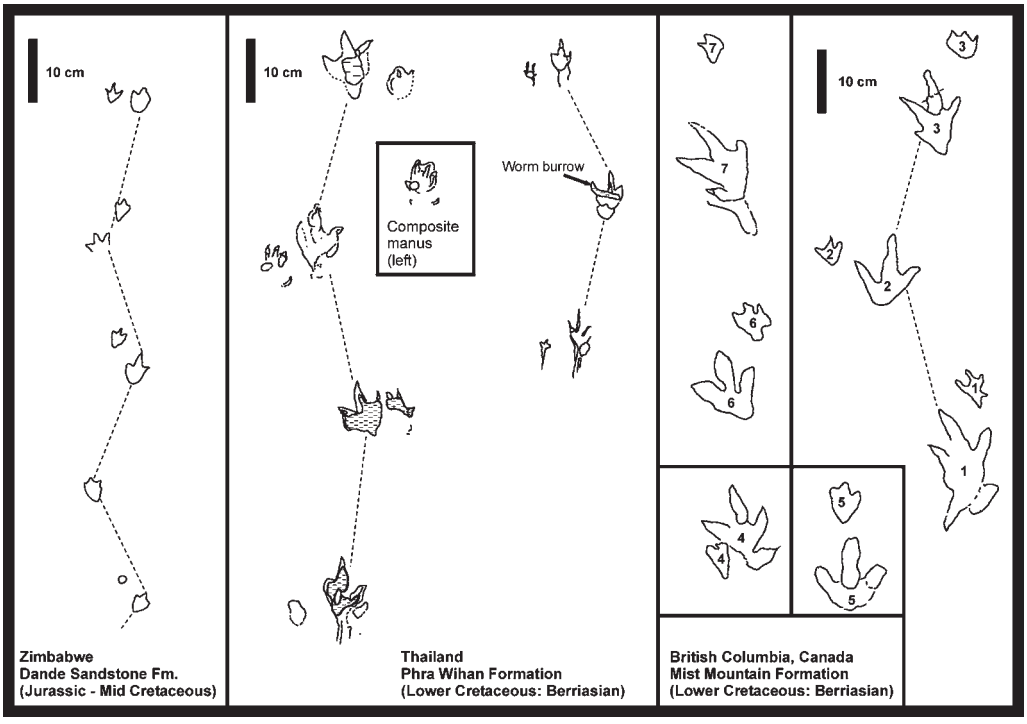

Fig. 8. From left to right: comparison between ornithischian trackways from Zimbabwe, Thailand and Canada. All drawn to same scale. Detail of holotype trackway of *Neoanomoepus* (far right) consists of a trackway segment of three manus–pes sets (1–3; preserved as replica FGM 002.01.20a and also as replica CU 199.22). Manus–pes sets numbered 4–7 include representative tracks from trackways B and C (compare with Fig. 5).

Anomoepodidae, which Lull (1953) attributed to an ornithopodan trackmaker. This ichnofamily originally contained only one ichnogenus (*Anomoepus*), which was traditionally considered to contain several ichnospecies (Lull 1953). However, Olsen & Rainforth (2003) considered that all ichnospecies within North America may be accommodated in *A. scambus* (however, for alternative views, see Lockley (2005) and Lockley & Gierlinski (2006)). The ichnogenus *Moyenosauripus* (Ellenberger 1974) has also been considered a synonym of *Anomoepus* by some workers (Olsen & Galton 1984; Olsen & Rainforth 2003), but a distinct ichnogenus by others (Gierlinski 1991; Lockley & Gierlinski 2006).

Anomoepus ichnospecies vary in size from about 5 to 15 cm (length of standing pes: *sensu* Lull 1953); that is, the length of the pes with hallux but without metatarsus impressions. However, metatarsus impressions are relatively common in *Anomoepus*. Olsen & Rainforth (2003, fig 19.18) identified one specimen that has a foot length of 19 cm (see Lockley 2005, fig. 2; Lockley & Gierlinski 2006). Among the features that distinguish the best-preserved material are the presence of a anteriomedially directed hallux and a distinctive pattern of double creasing between the digital pad impressions of the pes (see Lull 1953, figs 60, 62–67; Olsen & Rainforth 2003, figs 19.4–19.5). Some specimens also reveal distinctive skin impressions consisting of fine circular tubercles that are very regular in size and shape, as seen, for example, on specimen 48/1 in the Hitchcock collection. The manus impression, according to Lull (1953), also exhibits five digit impressions with distinct digital pad traces. The step is relatively short and the axis of digit III of the pes rotates inwards. Left and right tracks are clearly distinguishable, with a moderately wide trackway (about twice as wide as footprint width) and pes pace angulation values of between 130° and 150° (Fig. 1).

Although some specimens in the Hitchcock collection show the fine clear detail indicated by Lull (1953) in his line drawings, most do not. For example, there are many trackways of *Anomoepus* that indicate bipedal progression, and even where manus impressions are preserved it is hard to see all five digit impressions as clearly as Lull's drawings indicate. These deficiencies are rectified to some extent by the work of Olsen & Rainforth

(2003), whose illustrations are a great improvement on Lull's artwork. One also does not see the pes hallux impression (digit I) in many tracks, and many also do not show metatarsal impressions. Such variability is to be expected in a large sample and can be attributed to variable preservation and/or variability in mode of progression.

When we compare these classic Liassic *Anomoepus* tracks with those found in the basal Cretaceous sequences of British Columbia and Thailand there are clearly some distinctive similarities. The tracks fall in the same general size range (between about 5 and 12 cm pes length) with short steps, inward rotation of pes digit III and pace angulation values averaging about 140°. However, the tracks are also different in a number of respects. Most notably, despite good preservation in multiple examples, the tracks appear to lack discrete digital pad impressions on either the pes or the manus, in most cases. This could be attributed to preservation, but given that the much smaller manus tracks show all five digit impressions, a phenomenon rarely seen in the Hitchcock collections, Lull's artwork notwithstanding, we interpret this as a primary feature. It has been noted that many dinosaur track types reveal a trend of increased fleshiness with time (Lockley 1999, 2000; Lockley *et al.* 2000). Thus, it is most parsimonious to infer that the lack of discrete pad impressions separated by double creases, as in *Anomoepus*, is a primary feature of morphological, and hence ichnotaxonomic significance. It also appears that in Cretaceous material from Canada and Thailand the hallux is directed more anteriomedially and may also be more anteriorly situated than in the type material of *Anomoepus*. Also, despite their depth, which is generally greater than Early Jurassic *Anomoepus*, the Cretaceous tracks also consistently lack full metatarsus impressions in most cases. This suggests that the Cretaceous forms may have been more digitigrade than basal ornithischians. It is for these reasons that we propose a new ichnogenus: *Neoanomoepus*, accommodated in the ichnofamily Anomoepodidae.

Another feature of the Cretaceous trackways is that they appear to represent quadrupedal progression in a majority of cases despite the small size of the sample in comparison with the Jurassic material. Although it is debatable whether this should be considered a significant factor in formal ichnotaxonomy, on balance, the distinction between biped and quadrupeds is generally taken to be of prime importance in ichnotaxonomic descriptions. Regardless of opinion on this issue it is worth pointing out that quadrupedal progression appears to be more common among Cretaceous ornithopods than among their Jurassic ancestors, and in this sense the tendency towards becoming facultative quadrupeds is significant if not absolutely diagnostic.

Systematic descriptions

Ichnofamily Anomoepodidae Lull 1953
Emended Gierlinski 1991

Ichnogenus *Neoanomoepus* ichnogen. nov. (Figs 4–6, 8)

Diagnosis. Small trackway of a quadruped with tetradactyl pes larger than pentadactyl manus. Pes axis inwardly rotated and pes digit I short and anteromedially directed. Manus outwardly rotated and situated lateral to pes digit III or IV. Step short and trackway irregular.

Ichnospecies *Neoanomoepus perigrinatus* ichnosp. nov. (Figs 4–6, 8, Table 1)

Description. Small trackway of a quadruped with tetradactyl, slightly elongate pes (mean length 13.2 cm excluding short heel or metatarsal trace; mean width 11.1 cm), which is much larger than the pentadactyl manus (mean length 3.6 cm; mean width 6.0 cm). Pes axis inwardly rotated between 10 and 25° from trackway mid-line and pes digit I short and anteromedially directed. Manus outwardly rotated and situated lateral to pes digit III or II. Step and stride short (mean step 31.1 cm and mean stride 49.5 cm for three trackways on type slab; see Table 1). Trackway, trackway width and pace angulation irregular. Mean pace angulation 122° (range 90–143°, $n = 8$). Trackway width greater for manus (mean 27.2, range 19.5–34.8 cm) than for pes (mean 24.5 cm, range 19.3–34.2 cm, $n = 6$).

Etymology. Meaning 'new *Anomoepus*' that travelled widely.

Type material. Holotype- and paratype-bearing original slab still in field on 'crown' land, but mould and replica of complete slab in Fraser–Fort George Regional Museum (FGM 002.01.20). Trackway A is designated as the holotype trackway (FGM 002.01.20a), with an additional replica of holotype trackway A (CU 199.22) in the University of Colorado at Denver, Dinosaur Tracks Museum. Trackway B is designated as a paratype trackway (FGM 002.01.20b), with additional replica of trackway B (CU 199.23) in the University of Colorado at Denver, Dinosaur Tracks Museum.

Type locality. Elk Valley Coal region, SE British Columbia, Canada.

Type horizon and age. Mist Mountain Formation, Berriasian.

Distribution and probable affinity of *Neoanomoepus*

Various workers have attributed *Anomoepus* to a basal ornithischian trackmaker or more specifically to an ornithopod. However, there are no known Early Jurassic ornithopod trackmakers with splayed manus digits that would fit the *Anomoepus* manus footprint. Compelling ichnological evidence of ornithischian affinity in either the Jurassic or the Cretaceous generally depends on the occurrence of quadrupedal trackways, because tracks made by bipeds are generally less diagnostic. A distinction can be made between ornithischian tracks that display marked heteropody (pes much larger than manus), which are usually attributed to basal ornithischians and ornithopods, and those with less pronounced heteropody (pes and manus more equal in size), which are usually attributed to thyreophorans or ceratopsians. Based on this general distinction, *Neoanomoepus* seems to be of ornithopod affinity because basal ornithischians are not recorded in the Cretaceous, whereas ornithopod are present and diverse.

At present very few tracks of quadrupedal ornithischians are known from the Jurassic. *Anomoepus*, rare *Delatorrichnus* and an unnamed track from Asturias, Spain, are the only quadrupedal trackmakers with strong heteropody so far reported. Thus we infer that there is a significant gap in the distribution of Anomoepodidae between the early Jurassic and the early Cretaceous. Jurassic ornithischian tracks that demonstrate less heteropody such as an unnamed trackway from the Early Jurassic of France (Le Loeuff *et al.* 1999) or *Deltapodus* (Whyte & Romano 2001) from the Middle Jurassic of England, and a similar unnamed form from the Late Jurassic of Spain (García-Ramos *et al.* 2004; Gierlinski & Sabath 2009), are still poorly known and mostly without accepted ichnotaxonomies.

Canadian type *Neoanomoepus* occurs in strata that are well dated as Berriasian. Likewise, similar trackways from Thailand, which we herein refer to as *Neoanomoepus* sp., have also been assigned a Berriasian age. Such correlations may be coincidental but they may also indicate an early Cretaceous ornithischian radiation. As noted above, this inference arises from the scarcity of small *Anomoepus*-like quadrupedal ornithischian traces in the Middle and Late Jurassic, followed by a pronounced Early Cretaceous radiation of ornithopods, many of which, based on tracks, were quadrupedal. Thus, the appearance of *Neoanomoepus* in the earliest Cretaceous suggests that the Early Cretaceous radiation of ornithopods, and ornithischians in general, involved small as well as large species. Recent discoveries in British Columbia indicate that 'Anomoepodidae-like' tracks (Fig. 9) also occur in the Gorman Creek Formation of Valanginian age stratigraphically above the Mist Mountain Formation (McCrea & Buckley 2005*b*, 2006). This supports the inference of diverse ornithopod ichnofaunas becoming more prevalent in the early Cretaceous.

For a comprehensive review of available ichnological evidence it is necessary to compare *Neoanomoepus* with other purported ornithopod or ornithischian tracks made by small bipeds, or quadrupeds that exhibit extreme heteropody. The only tracks that fall in this category are Early–Middle Jurassic *Delatorriichnus* tracks (Casamiquela 1964; Gierlinski *et al.* 2004) and *Dineichnus* footprints (Lockley *et al.* 1998) from the Late Jurassic. The latter ichnogenus has been attributed to a dryomorph trackmaker (Fig. 7). *Hypsiloichnus* from the Early Cretaceous, as the name implies, is inferred to be of hypsilophodontid origin (Stanford *et al.* 2004). There are significant morphological differences in all these cases. *Delatorriichnus* possesses a tridactyl manual print reminiscent of heterodontosaurid morphology. *Dinehichnus* has no trace of a functional pes digit I, and no manus impressions, whereas *Neoanomoepus* has a short pedal digit I and small pentadactyl manual impressions. *Hypsiloichnus* differs from both these ichnogenera in having a more elongate pes, longer pedal digit I and very small manual impressions (Fig. 10); however, it is not known from a trackway sequence. These differences help justify the different ichnogenus designations, and suggest that *Neoanomoepus* was not made by either the trackmaker of *Delatorriichnus*, *Dineichnus* or *Hypsiloichnus*.

The unnamed trackmaker from the Cerradicas site in Spain has a pedal morphology and inward rotation similar to large *Dinehichnus* (Lockley *et al.* 1998), which in turn is similar to *Asianopodus* (Matsukawa *et al.* 2005). The elongate foot, sharp claw traces and phalangeal pad segmentation of the Cerradicas tracks means that they could easily be mistaken for a theropod if it were not for the presence of manus tracks. However, the inward rotation of the pes and rounded symmetric heel pad, which are also features of *Dinehichnus* tracks are typical of ornithopods.

As indicated above, the inner pes digit (I) of the trackmakers of *Neoanomoepus* and *Hypsiloichnus* (Fig. 10) was long enough to make contact with the substrate, although this was not the case with the maker of *Dinehichnus* tracks. A well-developed hallux (digit I) is typical of the primitive condition seen in basal ornithischian, basal thyreophorans and basal ornithopods, as well as in hypsilophodontids (Weishampel *et al.* 2004), which may have included the maker of anomoepodid tracks (Olsen & Rainforth 2003). In contrast, the lack of a pes hallux in more derived large ornithopods

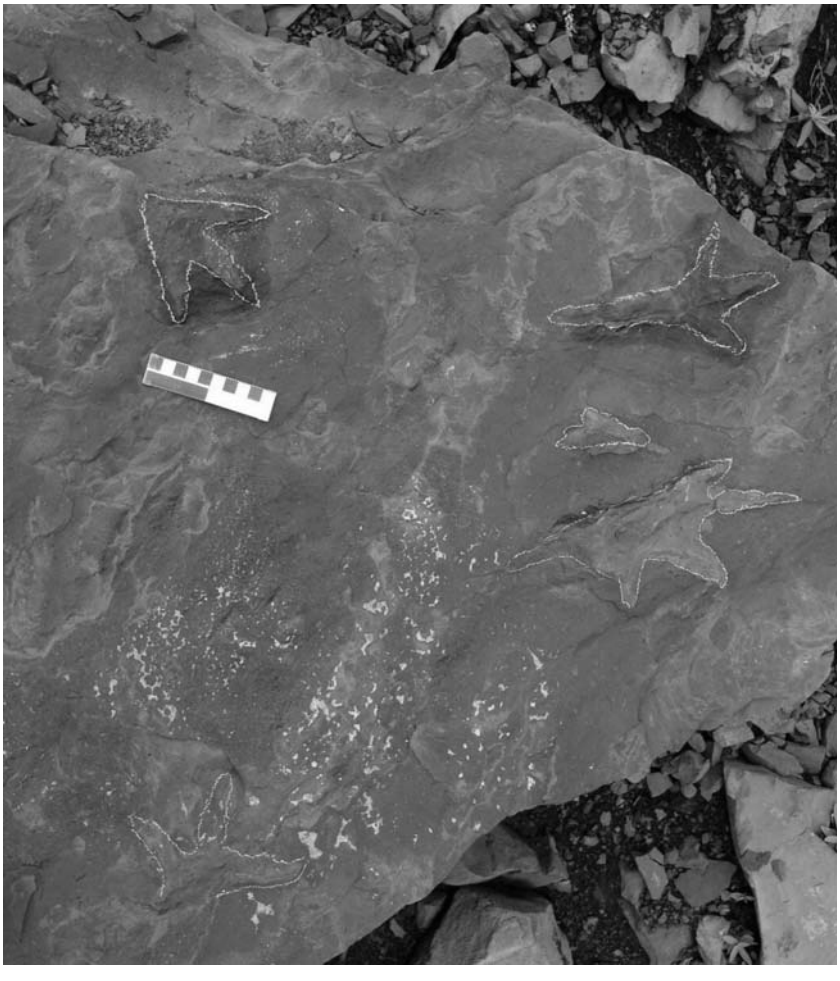

Fig. 9. 'Anomoepodidae tracks' from the Gorman Creek Formation (Valanginian) British Columbia. It should be noted that these tracks, unlike those from the Mist Mountain Formation, show metatarsal traces and one shows phalangeal pad impressions on pes digit III.

(iguanodontids and hadrosaurs) and their tracks and in some other ornithischians (ankylosaurs) is well known (Weishampel *et al.* 2004). The track record supports this by showing that small forms inferred to be ornithopods retained the primitive digit I. In contrast, traces of this digit are never found in large ornithopod tracks, although they are common in many other ornithischian tracks. This shows that the track and bone records consistently provide evidence of the reduction of pes digit I in some clades of large ornithopods and among some other ornithischian tracks.

The track record is also helpful in showing us the significant reduction of manual digits I and V among ornithopods. However, we know of no examples of track evidence for such significant reductions among other ornithischians. In the Early Cretaceous, the manus tracks of *Neoanomoepus*, the Cerradicas specimens (Perez-Lorente *et al.* 1997) and various iguanodontid tracks such as *Iguanodontipus* (Sarjeant *et al.* 1998), *Caririchnium* (Leonardi 1984; Lockley 1987; Lockley & Wright 2001), *Amblydactylus* (Currie & Sarjeant 1979) and *Hadrosauropodus* (Lockley *et al.* 2004) show clear evidence of the reduction of digits I–V to produce pronounced heteropody in comparison with other ornithischian tracks. Associated with this small manus we see an amalgamation of digits II, III and IV into an integument whose distal end made hoof-like impressions. In short, as the trackmakers became larger their feet became more fleshy. Such morphological shifts are size-related and involve a

Fig. 10. A *Hypsiloichnus* manus and pes set: modified after Stanford *et al*. (2004).

shortening of distal phalangeal elements while the proximal elements (metatarsals and metacarpals) lengthen in compensation.

This trend of reduction in number of digits, coupled with reduction of distal elements, and a shortening and broadening of the foot is not unique to ornithopods. It has been noted in the saurischian clade (Lockley 1999, 2001; Lockley *et al*. 1997) and even parallels the evolution of the foot in Tertiary ungulates, notably the equids. Thus, the trend in Early Cretaceous ornithopods, whether small, intermediate or large sized, is towards greater, functional digitigrady.

Available ichnological information for presumed ornithopods generally supports this trend. Thus, Early Jurassic *Anomoepus* shows the highest incidence of metatarsal impression (pes plantigrady) and pentadactyl manus traces. Younger Late Jurassic and Early Cretaceous tracks show a number of trends towards digit reduction and greater digitigrady. In smaller Cretaceous ichnotaxa such as *Neoanomoepus* and *Hypsiloichnus* such trends are not pronounced. Traces of a functional digit I indicate minimal digit reduction and attest to a primitive, more-plantigrade condition similar to *Anomoepus*, although without strong evidence of plantigrady in metatarsal posture. The other 'derived' trend is more pronounced and involves the conspicuous reduction of lateral digits I and V in both the pes and manus. Digit I reduction in the pes is confirmed by body fossils (Weishampel *et al.* 2004). Although, based on skeletal evidence, manus digit reduction is less pronounced, manus traces are nevertheless highly diagnostic because of the evidence of extreme digitigrady. This is most pronounced in intermediate- and large-sized species, which developed a small hoof-like manus.

The similarity between Early Jurassic *Anomoepus* and Early Cretaceous *Neoanomoepus* tracks suggests iterative radiations of small ornithopods on at least two occasions, although during the early Cretaceous there was a major radiation of large ornithopods. We infer that these evolutionary events left a discernible ichnological record of trackways attributable to both quadrupeds and bipeds that are best attributed to ornithopods rather than to other ornithischians. Despite the convergence suggested by the names and descriptions, the tracks from these two periods (near the Triassic–Jurassic and Jurassic–Cretaceous boundaries; at about 208 and 145 Ma, respectively) can be differentiated on minor morphological grounds.

These occurrences suggest two acme zones representing significant radiations some 60–65 Ma apart. In this regard the track record is consistent with the skeleton record of an earliest Cretaceous radiation of ornithopods involving both small clades such as the hypsilophodontids and large clades such as the iguanodontids (Weishampel *et al.* 2004). This convergence of the skeletal and ichnological records inspires confidence in the utility of both for recording macro-evolutionary trends.

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